

Micromorphology and microstructure as expressions of scleractinian skeletogenesis in *Favia fragum* (Esper, 1795) (Faviidae, Scleractinia)

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ABSTRACT

Microstructural differences observable within septa are currently recognized as major phylogenetic criteria among Scleractinia. If the emergence of molecular techniques provides a good mean of assessing these criteria, some recent results using molecular approach seem to give only low support for microstructural-based phylogenetic relationships of Scleractinia. This, however, may result from the numerous uncertainties concerning the microstructural pattern of species upon which major taxa are based. Three-dimensional characters of septal growth units and their variability have here been investigated using the specimens of *Favia fragum* included within the Milne Edwards Collection, these being the oldest reference material still available today. Integrating these data with results from the most recent work on this species leads to the reconstruction of the three-dimensional pattern of septal architecture. The phylogenetic significance of this requires assessment with alternative approaches.

KEY WORDS

Favia fragum,
Scleractinia,
skeletogenesis.

RÉSUMÉ

Micromorphologie et microstructure chez Favia fragum (Esper, 1795) (Faviidae, Scleractinia) en tant qu'expressions de la squelettogenèse des scléractiniaires.

Chez les scléractiniaires, ce sont actuellement les différences microstructurales observables dans les septes qui sont reconnues comme critères phylogénétiques majeurs. Si l'émergence des méthodes moléculaires fournit des moyens d'évaluer ces critères, des résultats récents utilisant l'approche moléculaire semblent donner seulement une faible valeur à la phylogénie des scléractiniaires fondée sur les microstructures. Ceci, toutefois, peut résulter des nombreuses incertitudes concernant les microstructures des espèces sur lesquelles les taxons majeurs sont basés. Les caractéristiques tridimensionnelles des unités de croissance septales et leur variabilité ont été ici étudiées sur les spécimens de *Favia fragum* de la collection Milne Edwards, qui sont le plus ancien matériel de référence actuellement disponible. La prise en compte de l'ensemble des données résultant des recherches plus récentes concernant cette espèce permet la reconstitution tridimensionnelle de l'architecture septale. La signification phylogénétique de ce type d'analyse devra être évaluée par rapport aux résultats obtenus par les approches concurrentes.

MOTS CLÉS

Favia fragum,
Scleractinia,
squelettogenèse.

INTRODUCTION

As pointed out by Veron *et al.* (1996) the well known Wells' evolutionary tree for Scleractinia "has long been in need of revision". This is well shown by important discrepancies existing between the highest taxonomic subdivisions of the alternatively proposed evolutionary schemes of Scleractinia, even when considering only the most recent hypotheses of Veron himself (1995), Roniewicz & Morycowa (1993) and Chevalier & Beauvais (1987).

Pioneered by Pratz (1882), Ogilvie (1896) and numerous others, description of fibre arrangements in corallian structures soon became recognized as a prominent tool in coral taxonomy and later, was formally regarded of fundamental importance by Wells (1956: fig. F237, F340). By contrast, recent DNA sequencing studies led Veron *et al.* to the conclusion that "morphological characters of extant corals distinguish families more reliably than do internal microskeletal characters frequently used in coral paleontology" (1996: 1). If true, this conclusion should lead to a basic methodological change in the taxonomic approach to the scleractinian skeleton.

Numerous obscure points still persist in the

microstructural knowledge of the "key species", i.e. the type species for the genera on which families are based. Therefore, microstructural study of these "key species" is a prerequisite for critical reexamination of related supra-specific taxa.

Among these "key species", *Madrepora fragum* Esper, 1795 the type species of the genus *Favia*, is one of the most important, as it is the type genus for one of the major scleractinian taxa: the family Faviidae, and the suborder Faviina (Triassic to Recent). In addition, this species also illustrates the poor state of basic microstructural data. In most cases, precise descriptions of septal growth including recent improvement in understanding of biomineralization processes are completely lacking. This cannot constitute a reliable consistent basis for taxonomic considerations.

The aim of this paper is therefore to present an accurate description of the type species *Madrepora fragum* in the light of recent knowledge of scleractinian skeletogenesis. Emphasis is especially placed on integrating morphological, micromorphological and microstructural data in order to provide a better understanding of the three-dimensional skeletal growth process. These analyses have been carried out on the *Favia fra-*

gum colonies of the Milne Edwards Collection housed at the Muséum national d'Histoire naturelle of Paris. Because the type specimen of *Favia fragum* is now lost, the material of Milne Edwards represents today the most relevant specimens from an historical point of view.

SUMMARY OF PREVIOUS STUDIES

NOMENCLATURE

Originally created by Oken (1815), the genus *Favia* was included in the rejection by the ICZN of all taxa proposed in the Oken's book (decision 417). However, the genus group name *Favia* was made available by the work of Milne Edwards (1857) who used it for a group of species including *Madrepora fragum* Esper, 1795. Verrill (1902) designated *Madrepora fragum* as type species of the genus *Favia*. From a formal point of view, the genus name *Favia* should be considered as *Favia* Milne-Edwards, 1857 [not Oken, 1815].

Concerning the choice of *Madrepora fragum* Esper, 1795 as type species of *Favia* by Verrill (1902), Alloiteau (1957) and later Zlatarski & Martinez Estalella (1982) followed Verrill's proposal although *Madrepora fragum* Esper, 1795 is considered as a posterior synonym of *Madrepora ananas* Pallas, 1766. Verrill (1902: 90) emphasized that the use of *ananas* could introduce confusion since the name *Madrepora ananas* was already used by Linnaeus (1758) for a Palaeozoic coral from Gotland now belonging to the genus *Acervularia* Schweigger, 1819 and also applied to extant species by earlier authors (not mentioned in the Verrill's paper).

Since Milne Edwards (1857), the genus *Favia* gained in taxonomic importance as it was designated as type genus of the Faviidae by Gregory, 1900 and the family Faviidae considered as the basis for the suborder Faviina Vaughan & Wells, 1943.

In the first publication of *Favia fragum* (Esper, 1795), Esper although not using conventional terms for describing coral specimens, referred to the geometry of the calices, the wall structure and even the distal margin of the septa with surprising precision. This type specimen which was

sampled from Recent reefs of the Caribbean, is now lost (Zlatarski & Martinez Estalella 1982). Milne Edwards & Haime (1849), describing a Recent specimen from Haiti, provided more detailed information about the geometry and structure of the calices. These especially concern intracalicular budding, septal arrangement in four cycles and the distal margin of major septa showing a well-developed tooth at the axial margin. The specimen was referred to *Parastrea fragum* by the authors (Milne Edwards & Haime 1849) but later transferred to the genus *Favia* by Milne Edwards (1857). Subsequent morphological descriptions of this species are numerous, including observations on the living tissues (e.g. Duerden 1902; Matthai 1919).

THE FIRST MICROSTRUCTURAL ANALYSIS OF *FAVIA FRAGUM* BY ALLOITEAU (1957)

Alloiteau was the first to analyse the microstructure of *Favia fragum* from thin sections. According to this author, septal and costal microstructures slightly differ. The costal part is formed by very large and simple trabeculae (Alloiteau 1957: 138, "poutrelles"), clearly separated from each other by a thin denticulate sutural line. Each trabecula seen in transverse thin section contains a large calcification centre consisting of several dark dots from which aragonitic fibres radiate. The septal part shows smaller trabeculae with less well-defined borders and the calcification centres are sometimes so close that they form a thick subcontinuous median dark line. Additional calcification centres also occur on both sides of this median line. Aragonitic fibres radiate from each centre and are perpendicular to the lateral faces of septa.

THE STUDY OF *FAVIA FRAGUM* BY ZLATARSKI & MARTINEZ ESTALELLA (1982)

Based on detailed observations of an extensive collection from Cuba, the work of Zlatarski & Martinez Estalella (1982) provides one of the most comprehensive studies of *Favia fragum*, including description of the successive stages of the budding process and assessment of intraspecific variability. In particular, calicular arrangement, usually regarded as a generic character of *Favia* [plocoid, Wells (1956); subplocoid,

Alloiteau (1957)], appears to be highly variable. The calicinal surface may be plocoid, cerioid or meandroid and often shows intermediate stages between these various arrangements. Other variable characters observed by these authors, include calicinal size, ornamentation of peritheca, thickness of septa, abundance of septal dentation and columella development. Observations on the skeletal microstructure are in good accordance with the previous description of Alloiteau (1957). While in the costal part, the trabeculae within thin sections are well differentiated with irregular quadrangular periphery and large calcification centres, they gradually incline towards the septal axial margin forming a large dark median line in the central part of septa.

APPROACHES AND TECHNIQUES

Specimens of *Favia fragum* were successively observed on different scales and treated in several ways.

Morphological data were obtained from observations of each colony with a stereomicroscope. Detailed qualitative observations were related to measurements of geometrical characters usually regarded as standard criteria for scleractinian taxonomy.

Micromorphology and its variability were studied by scanning-electron microscopy (SEM). According to the morphological data, representative calices were selected within each colony and sampled using a dental saw. These samples were then coated with gold-palladium for 3D-observations with SEM.

Microstructure was studied in optical microscopy from the thin sections of the Alloiteau Collection housed at the Laboratoire de Paléontologie, MNHN, Paris.

Ultrastructural data were obtained by 2D-observation of transverse sections with SEM. Selected calices within each colony were cross-sectioned and polished with diamond paste. Several etching preparations of these surfaces were tried, in particular for precise observation of calcification centres and their internal structure. Some polished sections were treated with an enzymatic solution of alcalase, pH 7.5 for three hours at

35 °C with stirring of the preparation. A second set of samples was also prepared by etching with a solution of formic acid 0.1% and glutaraldehyde 3% for 40 seconds. Etched preparations were then coated with gold-palladium for SEM observation of ultrastructure. The latter was also compared with the microstructural data.

All SEM preparations are included in the Milne Edwards Collection housed at the Laboratoire de Biologie des Invertébrés marins et Malacologie, Muséum national d'Histoire naturelle, Paris.

DESCRIPTION OF *FAVIA FRAGUM* FROM THE MILNE EDWARDS COLLECTION AT THE MNHN

THE MILNE EDWARDS COLLECTION AT THE MNHN

This collection housed at the Laboratoire de Biologie des Invertébrés Marins et Malacologie (BIMM), Muséum national d'Histoire naturelle, Paris, comprises five specimens or groups of specimens sampled from diverse localities of the Caribbean. These are registered as follows:

FAV559, *Favia fragum* (Esper), Antilles (bought at Marseille), one small colony (Fig. 1A, B);

FAV560, *Favia fragum* (Esper), Haïti (Mr. Ricord, 1831), three small colonies and two fragments (Fig. 1C-H, K, L);

616, *Favia fragum* (Esper), Antilles (bought at Marseille, Mr. L. Rousseau, 1841), one small colony (Fig. 1M-O);

631, *Favia fragum* (Esper), Antilles (Mr. Roissy, 1837), one small colony (Fig. 1I, J);

1260, *Favia fragum* (Esper), Saint-Thomas (Mr. Duchassaing, 1870), one colony (Fig. 2A, B).

EXTERNAL SHAPE OF COLONY

The Milne Edwards specimens are small low colonies (about 4-10 cm in diameter and a few centimeters high) with globular, commonly hemispherical shape. The ovoid external morphology of two colonies (FAV560-1, 2) appears to be related to the elongated shape of their substrates, both consisting of a mytilid shell. The smallest specimens (FAV560-3, 4, 5) are low encrusting growth forms.

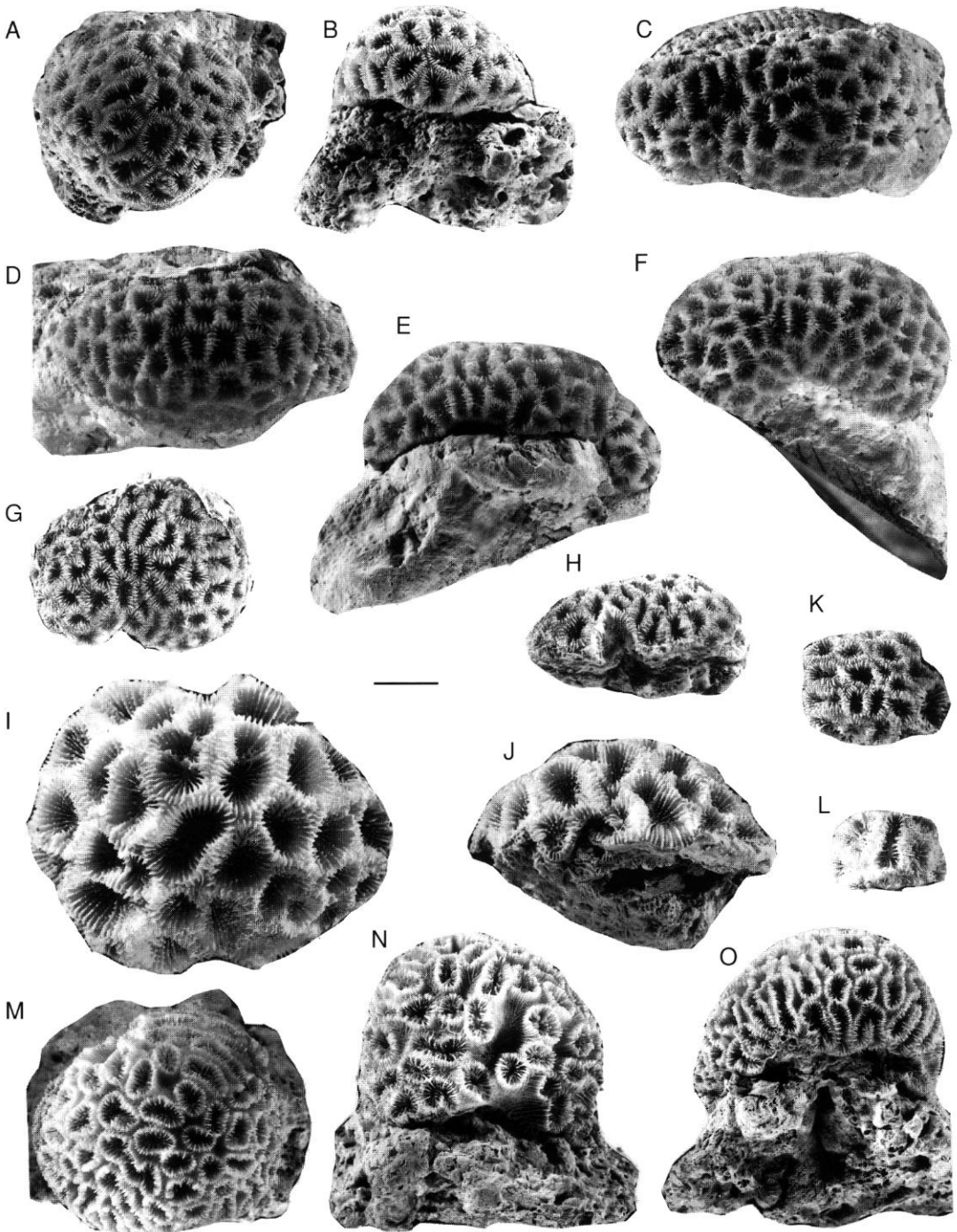


FIG. 1. — *Favia fragum* (Esper, 1795), specimens from the Milne Edwards Collection at the MNHN; **A, B**, specimen FAV559; **C**, specimen FAV560-1; **D, E**, specimen FAV560-2; **F**, specimen FAV560-1; **G, H**, specimen FAV560-3; **I, J**, specimen 631; **K, L**, specimen FAV560-4; **M-O**, specimen 616. Scale bar: 1 cm.

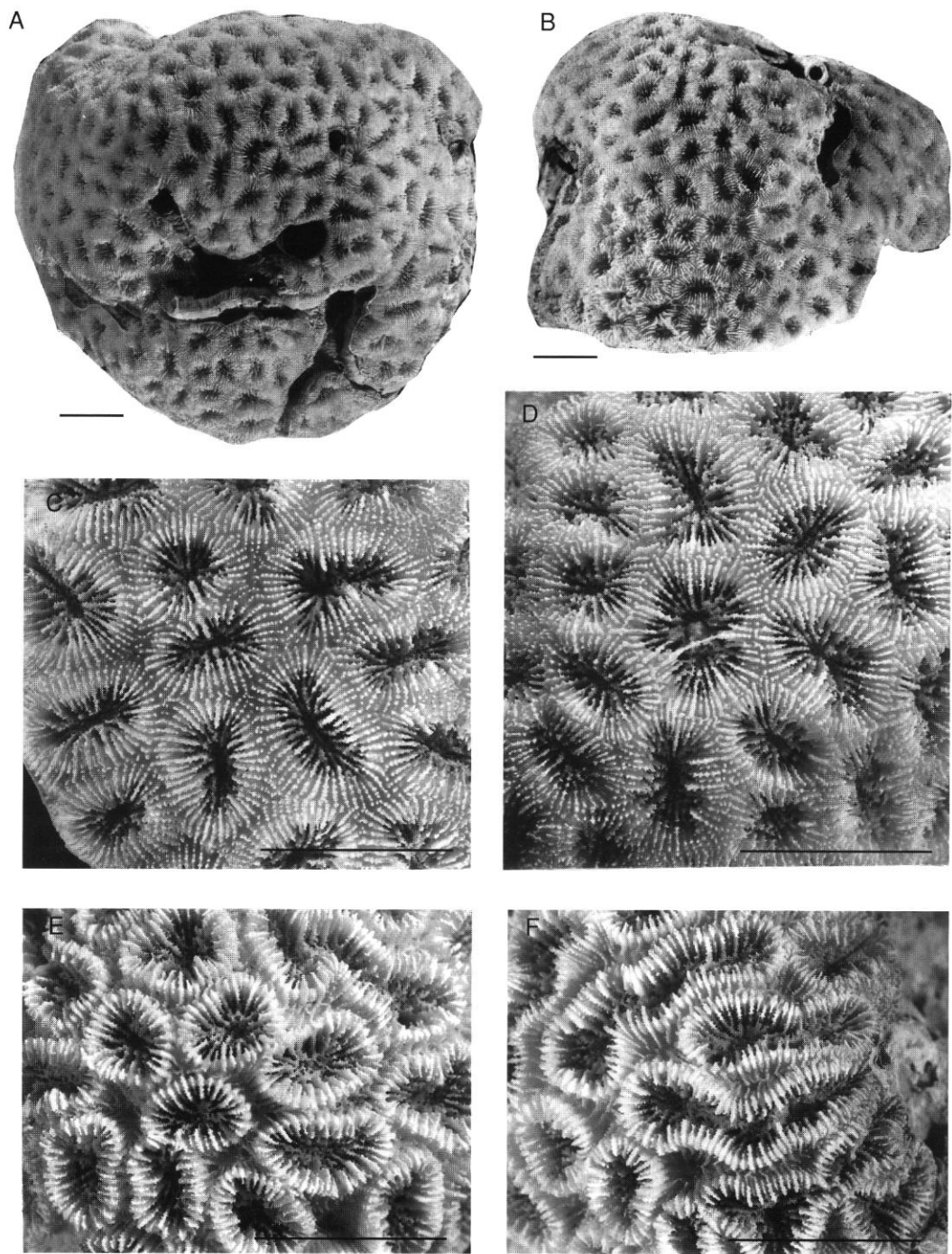


FIG. 2. — *Favia fragum* (Esper, 1795), specimens from the Milne Edwards Collection at the MNHN, calicinal relationships; **A-D**, specimen 1260; **C**, subploicoid part of colony; **D**, subcerioid part of the colony; **E-F**, specimen 616, **E**, ploicoid calices; **F**, part of the colony showing elongated meandroid calices. Scale bar: 1 cm.

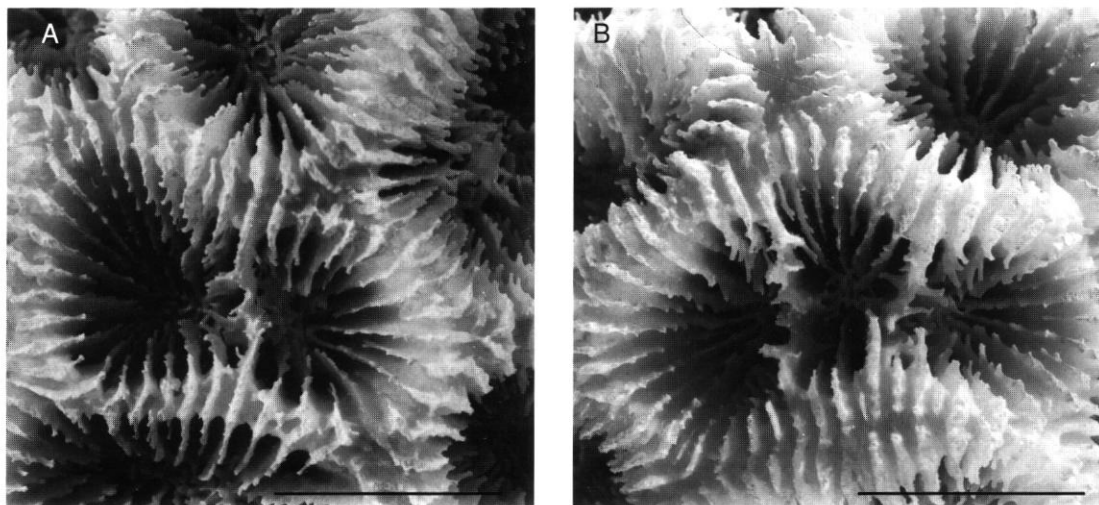


FIG. 3. — *Favia fragum* (Esper, 1795), budding, specimen 631; **A**, distomodeal budding; **B**, tristomodeal budding within the same colony. Scale bar: 1 cm.

CALICINAL RELATIONSHIPS

Colonies are usually plocoid (Fig. 2E), walls of individual calices being separated by dissepimental coenosteum. Distances between walls of neighbouring calices are however highly variable leading to a subplocoid or even a subcerioid (1260, Fig. 2C, D) appearance of colonies. Short series of calices are uncommon (FAV560-1, 2) although one specimen comprises some very elongated calices which tend to form short meanders at the periphery of the colony (616, Fig. 2F). Intracolony variability is high, even within the small colonies of the Milne Edwards Collection and calicinal relationship seems to be partly dependent on the position of calices within the colony.

BUDDING

Colony growth occurs through intracalicular usually distomodeal budding which results from subdivision of the mother calice into two approximately equal parts (Fig. 3A) or sometimes corresponding respectively to one third and two thirds of the initial calice. Division occurs through the axial development of two opposed major septa (commonly S1 or sometimes S2), axial margins of which gradually fuse until they form a distinct and compact separation. On each

side of this new wall, new septa are then developed resulting from twisting and growth of distal teeth of the initial septa. In some cases, both the opposite septa are twisted before becoming fused (631). Tristomodeal budding is rare (Fig. 3B) and results from the same process of subdivision into three equal parts. Polystomodeal budding may be observed on specimen 616 (Fig. 2F). In this case, centres are differentiated before the separation of young calices and series of up to five to six centres are formed. These parts of the colony tend to become meandroid.

CALICES

The most common calices are shallow with rounded or elongated shapes often distorted by intracalicular budding. Shapes of calices and distances between centres are, however, highly variable between colonies but also within the same colony. Calicinal shape varies from angular to subangular (FAV560), subpolygonal (631), up to very elongated meandroid calices (616). Occurrence of irregular calices usually increases towards the periphery of colonies. Diameter of adult monostomodeal calices averages 5-6 mm ranging from 4.5 to 7.5 mm in most colonies while their depth is around 1.5-2.5 mm. However, potential variability of calicinal size

and depth appears to be relatively high. Size of elongated meandering polystomodeal calices occurring within specimen 616 is about $10\text{--}15 \times 2\text{--}3$ mm. In addition, colony 631 shows much larger calices, diameter of which ranges from $10\text{--}14 \times 7\text{--}9$ mm (average 11.5×8 mm) with calicinal depth varying between 5 and 8 mm.

INTRACALICINAL STRUCTURES

Septa

Cycles, number of septa. Number of septa ranges from 32 to 54 within adult monostomodeal calices (Fig. 4A) and is about 40–41 on average. Septa are organized in four cycles with sometimes a few additional abortive septa contributing to the formation of the septothecal wall. The number of septal cycles appears very consistent within all studied colonies. Septa of the first two cycles (S1 and S2), equal or subequal, reach the columella. Septa of the third cycle are usually thinner and their development slightly varies between colonies. All or only some S3 may reach the calicinal centre; the other third-cycle septa extend to half to three quarters of the calicinal radius and may sometimes fuse with a neighbouring S2 at their internal border. The fourth cycle is incomplete, most of its septa being weakly developed and never exceeding one quarter of the calicinal radius. Septa correspond to costosepta and are usually straight or slightly curved. They are often gradually thinning from the calice periphery to the centre. Septa are compact although some pores may occur at their axial margin or even sometimes in their median part, those of the younger cycles being in general more porous than septa of the two first cycles. The overall septal porosity varies between colonies but seems to be similar within the same colony. Process of pore formation is clearly inferred at the axial margin in some calices. Pores are formed from the horizontal development of the uppermost internal tooth joining and further fusing with the vertically-extended axial tooth of the same septum, this leaving an empty rounded gap below the junction of both teeth.

Lateral faces of septa show conical-to-sharp points forming more or less regular lines parallel to the septal growth direction. Vertical near the calicinal wall, these lines are gradually inclined

towards the axial septal margin. Close to the distal margin, each line of points corresponds to the position of a distal tooth (Fig. 4B, C). Points on the lateral septal faces therefore result from the gradual burial of previous successive teeth within the incremental layers of fibrous aragonite contributing to the septal thickening.

Septal dentation. Teeth of the distal margin consist of groups of small points with a conical or curved, sharp or smooth shape located at the extremity of the tooth axis (Fig. 4D–F). The height of teeth regularly increases from the wall to the axial margin, the higher teeth developing at the uppermost internal and axial septal margin (Fig. 4B, C). Increase of tooth height occurs through the elongation of the dental main axis and not by the increasing size of the points. Teeth close to the calicinal periphery are subparallel to the wall while their inclination is gradually increasing towards the internal margin (Fig. 4C). In some calices, those of the uppermost internal margin are nearly horizontal. A strong axial tooth may also be developed vertically on those septa reaching the columella (i.e. mainly S1 and S2), these whole axial teeth forming within some calices a paliform crown around the columella. In some rare cases (631), the axial tooth may also be formed of its own small fan-system (Fig. 5F). Septa of the first two cycles bear stronger and better-developed dentation than those of the later cycles. Detailed observations of dental extremities reveal highly variable shape and organization within a given group of points (Fig. 5A–E). The ends of axial teeth and especially paliform teeth show a higher number of points with no preferential orientation while organization of the dental structure is gradually increasing towards the peripheral calicinal margin where points are progressively arranged in small paddle-like structures or fans oriented normal to the septal plan. The degree of organization is usually higher at the distal external margin of septa S1 and S2 but largely varies between calices and colonies. Some specimens never clearly show the paddle structure, even at the distal margin of major septa. By contrast, paddles are particularly common within specimen 631 (Fig. 6).

Microstructure. SEM observations of transverse

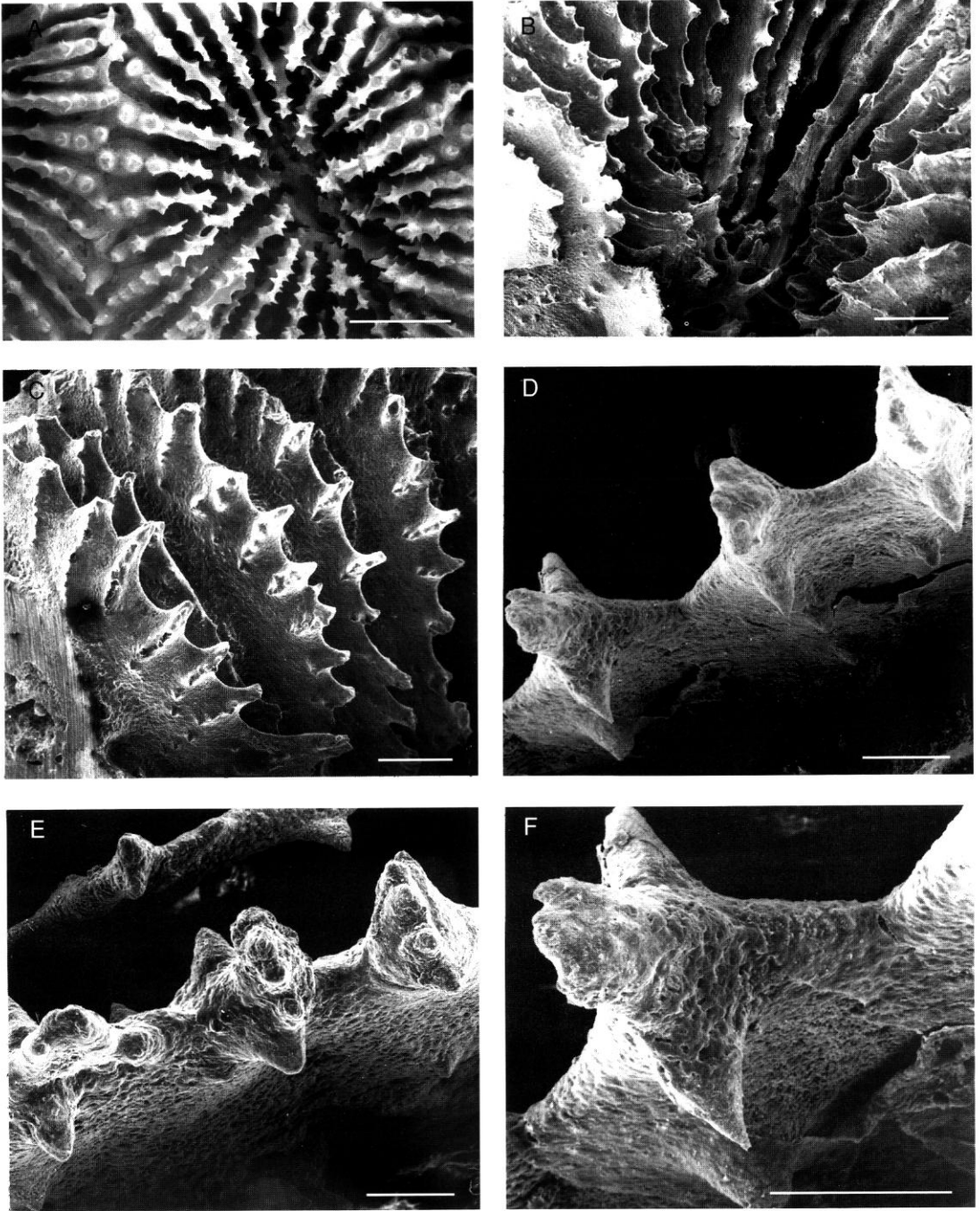


FIG. 4. — *Favia fragum* (Esper, 1795), SEM, distal margins of septa; **A**, specimen 1260, calice showing septal arrangement, columella and dentation of septal margins; **B**, **C**, specimen 631, **B**, internal part of a calice, shape and arrangement of distal teeth and formation of columella; **C**, part of a calice showing the gradational change of the shape and orientation of teeth at the distal margins of septa; **D-F**, specimen FAV560-1: **D**, middle part of a distal septal margin; **E**, more peripheral part of the distal margin; **F**, detail of **D**. Scale bars: **A**, **C**, 1 mm; **B**, 2 mm; **D-F**, 100 μ m.

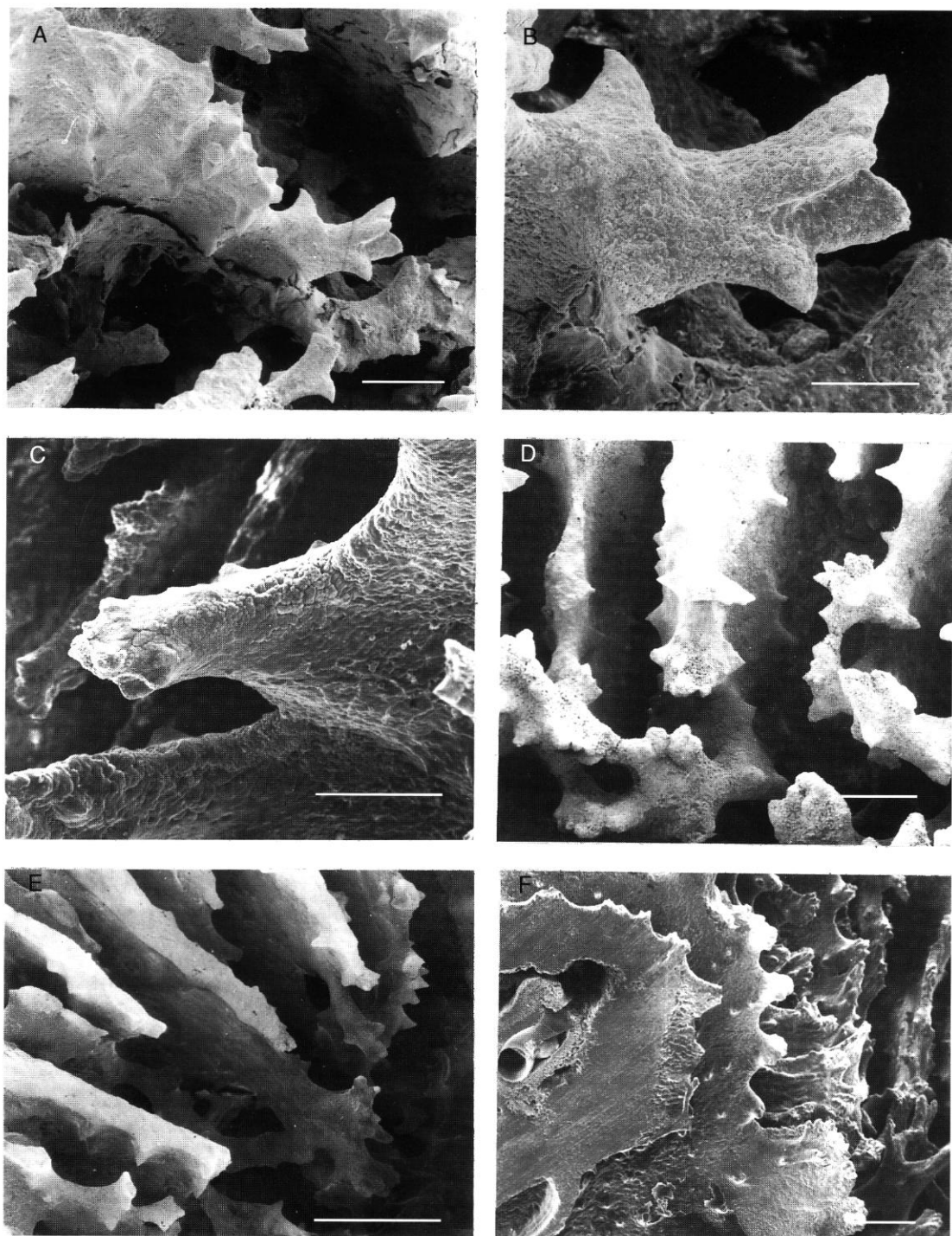


FIG. 5. — *Favia fragum* (Esper, 1795), SEM, variability of axial teeth; **A**, specimen FAV560-2; **B**, detail of A; **C**, specimen 631; **D**, specimen FAV560-4; **E**, specimen FAV560-5; **F**, specimen 631. Scale bars: A, D, 200 μ m; B, 100 μ m; C, E, 500 μ m; D, 200 μ m; F, 1 mm.

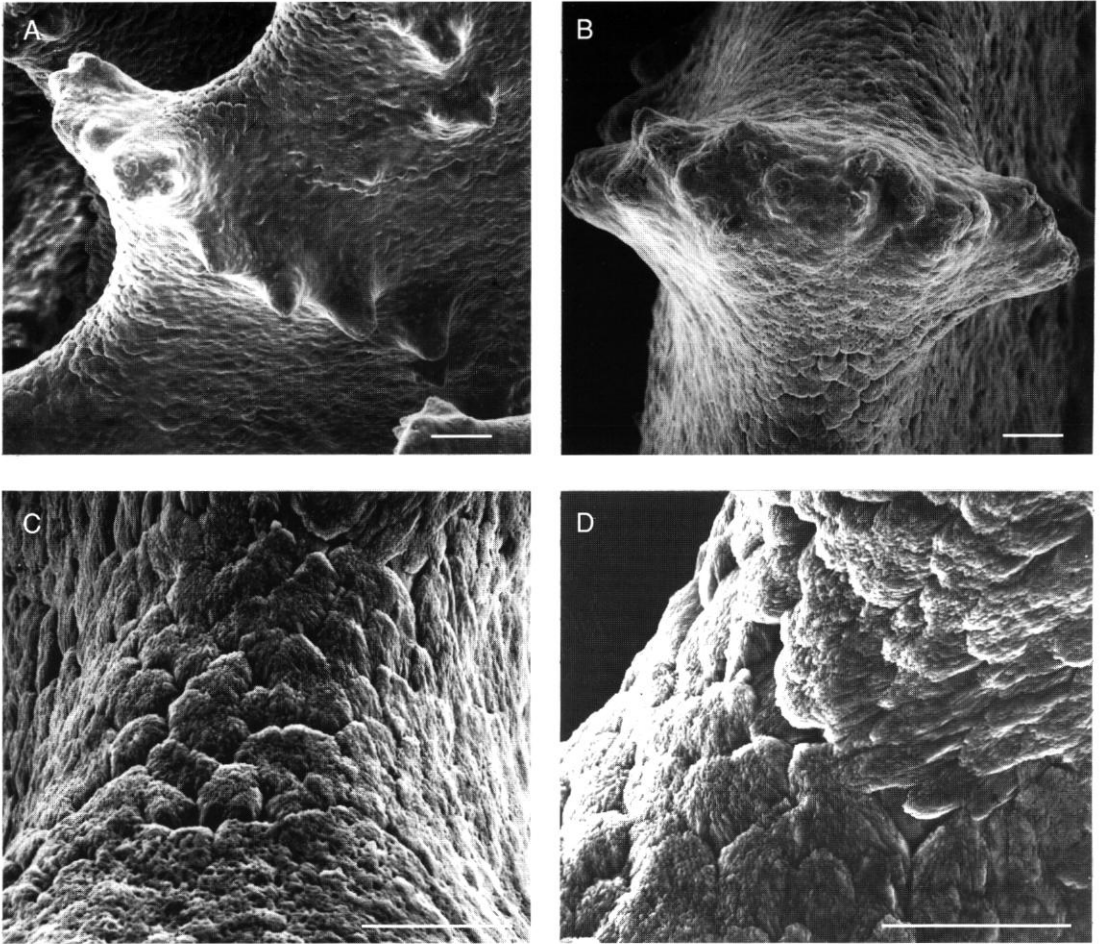


FIG. 6. — *Favia fragum* (Esper, 1795), SEM, relationship between ultrastructure and micromorphology, specimen 631; **A, B**, paddle-like tooth at the distal margin of septum, **A**, ornamentation of lateral face of septum is the result of gradational burial of lateral ends of teeth by successive incremental layers of aragonite; **C, D**, sets of aragonitic fibres seen between two neighbouring teeth at the distal margin of septum. Scale bars: A, 200 μ m; B-D, 100 μ m.

sections of septa taken at successively greater depth within the calice allow the internal structure and, therefore, the successive stages of septal growth to be understood (Fig. 7). Calcification centres appear as smooth round dots, about 25 μ m in diameter and devoid of fibres, but higher magnification shows that they consist of very small equant crystals. They are surrounded by concentric layers consisting of sets of fibres. Fibres are arranged approximately perpendicular to the layer boundaries. Orientation of fibres within the same layer slightly varies between adjacent sets but fibres of successive layers within

the same set have the same orientation (Fig. 8). Each layer records the successive incremental growth of coral skeleton. Fibre orientation through successive layers appears to be broadly consistent although growth direction may slightly vary between successive layers. Sets of fibres are also clearly distinguished on well-preserved distal surface of septa and obviously show a frequent oblique direction of fibres with respect to the growth surface (Fig. 6C, D).

Distribution of calcification centres within the septa clearly controls the external septal micromorphology and especially the formation of

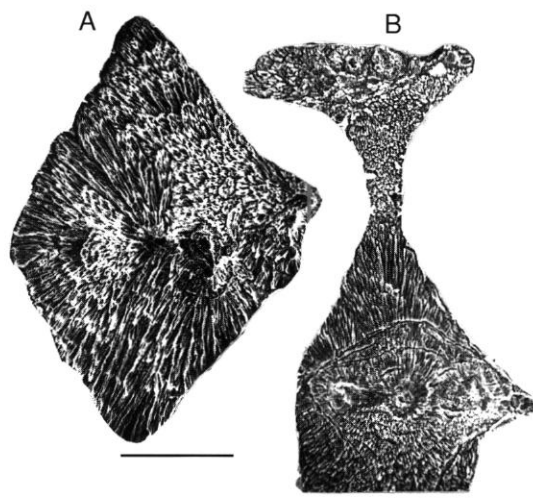


FIG. 7. — *Favia fragum* (Esper, 1795), SEM, ultrastructure of the distal margin, specimen 631; **A**, etched section of a tooth on the peripheral distal margin showing the line of calcification centres from which aragonitic fibres radiate; direction of calicinal margin is to the bottom of photograph; **B**, etched section of internal distal margin of a septum; differential development of aragonitic fibres is especially well shown within the younger incremental layers; direction of calicinal axis to the top of photograph. Scale bars: 200 µm.

teeth. Transverse sections through teeth show several calcification centres aligned roughly normal to the septal plan. Formation of teeth occurs through the development of aragonitic layers around these centres. Differential growth of aragonite fibres from each centre gradually fills up the space between two neighbouring teeth and junction of fibres showing opposite growth from successive teeth is usually well marked by an irregular line observed on SEM preparations and in thin sections (Fig. 8).

Columella

Columella is spongy and results from lateral development, twisting, fusion and tangling of axial margins and often axial teeth (Fig. 9A-C). Upper surface of columella may produce small spines similar to the dental points (Fig. 9C). When axial teeth are vertically oriented, they do not contribute to columella structure but tend to form a paliform crown. Diameter of columella varies between 1.3 to 2.5 mm, size and the density of structure both depending on the development of axial septal margins.

Endotheca

Endotheca consists of frequent thin interseptal dissepiments with a slight upward convexity. They are developed from lateral faces of neighbouring septa and do not occur at the same level across different interseptal spaces. Central junction *sensu* Sorauf (1970) within the interseptal space is marked by a little downward fold. Gently inclined close to the calicinal periphery, dissepiments tend to become subhorizontal to the centre.

WALL

Wall is continuous and mainly septothecal, formed by the thickening of septa in their external part but also by the adjunction of rudimentary radial elements developed from new calcification centres (Fig. 9D-F).

Etched transverse sections of wall under SEM show successive stages of wall formation. Development of wall begins by lateral growth of bars from opposing lateral faces of two neighbouring septa. This occurs through the formation of calcification centres at both lateral septal faces and incremental growth of fibres around each centre. These centres are roughly aligned normal to both septal planes and new centres are gradually added at each extremity of both convergent bars leading to their fusion (Fig. 10A). Thickening of this new wall results from the development of aragonite clusters around each centre but also, within the central part, from the adjunction of new calcification centres arranged perpendicular to the wall (Fig. 10B, C) and finally forming a rudimentary radial element.

EXOTHECA

Costae and costal dentation

Costae are usually well-developed, thicker than septa and non-confluent or subconfluent in most colonies, although specimen 631 shows frequent cases of costal confluence. Non-confluent costae of neighbouring calices are often separated by a narrow groove, previously mentioned by Zlatarski & Martinez Estalella (1982) but also by Esper (1795). When costae are subconfluent, this groove is more irregular and discontinuous. Costae corresponding to S1, S2 and S3 are longer than

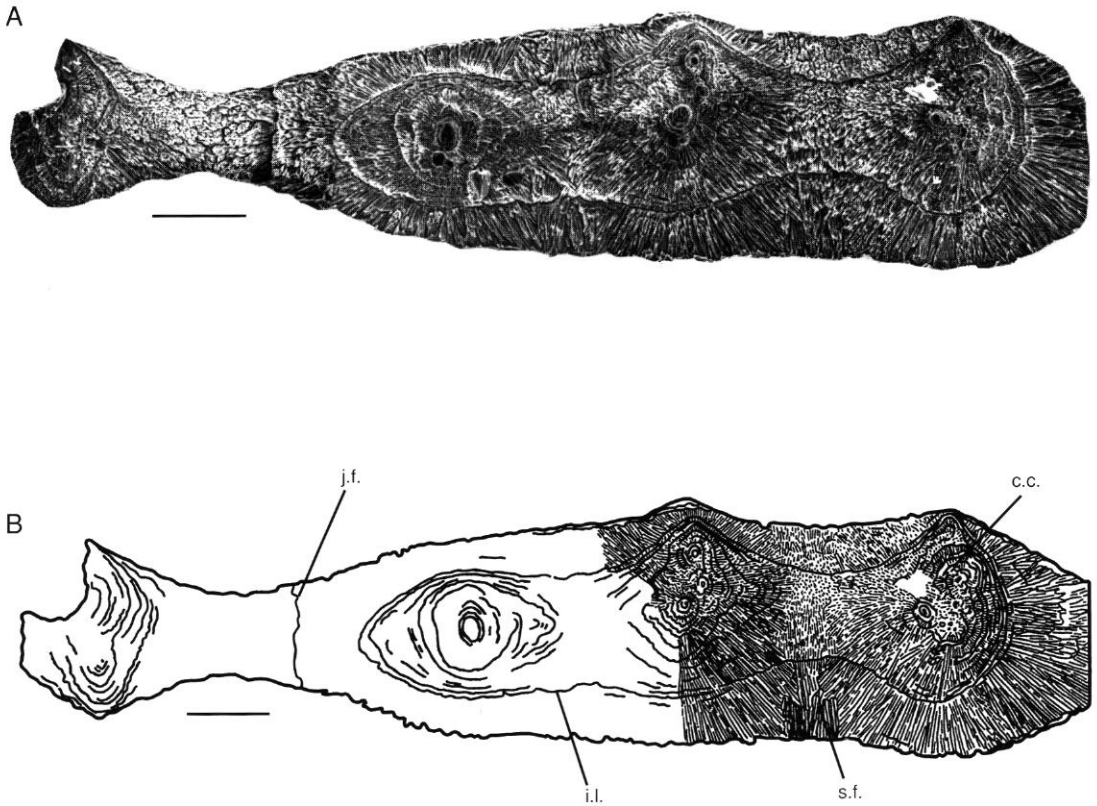


FIG. 8. — *Favia fragum* (Esper, 1795), ultrastructure of a septum; **A**, SEM, photomosaic of specimen 631; **B**, sketch traced from **A**; **c.c.**, calcification centres; **i.l.**, limit of incremental layer; **j.f.**, suture of fibres from neighbouring growth units; **s.f.**, sets of aragonitic fibres. Scale bars: 200 μ m.

those of the last cycle which are thick and short. Costal dentation (Fig. 11) comprises simple conical thick teeth close to the wall (Fig. 11B), while further from the calicinal margin, they are gradually inclined outwards and may develop a few small points at their distal end. Costal dentation, however, is never as well-developed as the septal teeth and the dental ends of costae often show random orientation of points (Fig. 11A). In particular, the paddle structure, which appears to represent the highest degree of dental organization, remains rare on costal teeth and was only observed in colony 631.

Coenosteum

Coenosteum consists of exothecal dissepiments similar in thickness and shape to their endothecal counterparts.

EPITHECA

Epithec is relatively thin and continuously surrounds the corallum external surface. Its ornamentation consists of numerous thin parallel transverse striations, sometimes slightly undulating. Morphological variability of epithec affects its thickness and continuity, and the intensity of its ornamentation.

THREE-DIMENSIONAL SKELETAL DEVELOPMENT OF *FAVIA FRAGUM*

CALCIFICATION CENTRES

Calcification centres have been defined as points from which aragonitic fibres radiate. Although their nature and composition as well as the exact process of calcification are still not fully under-

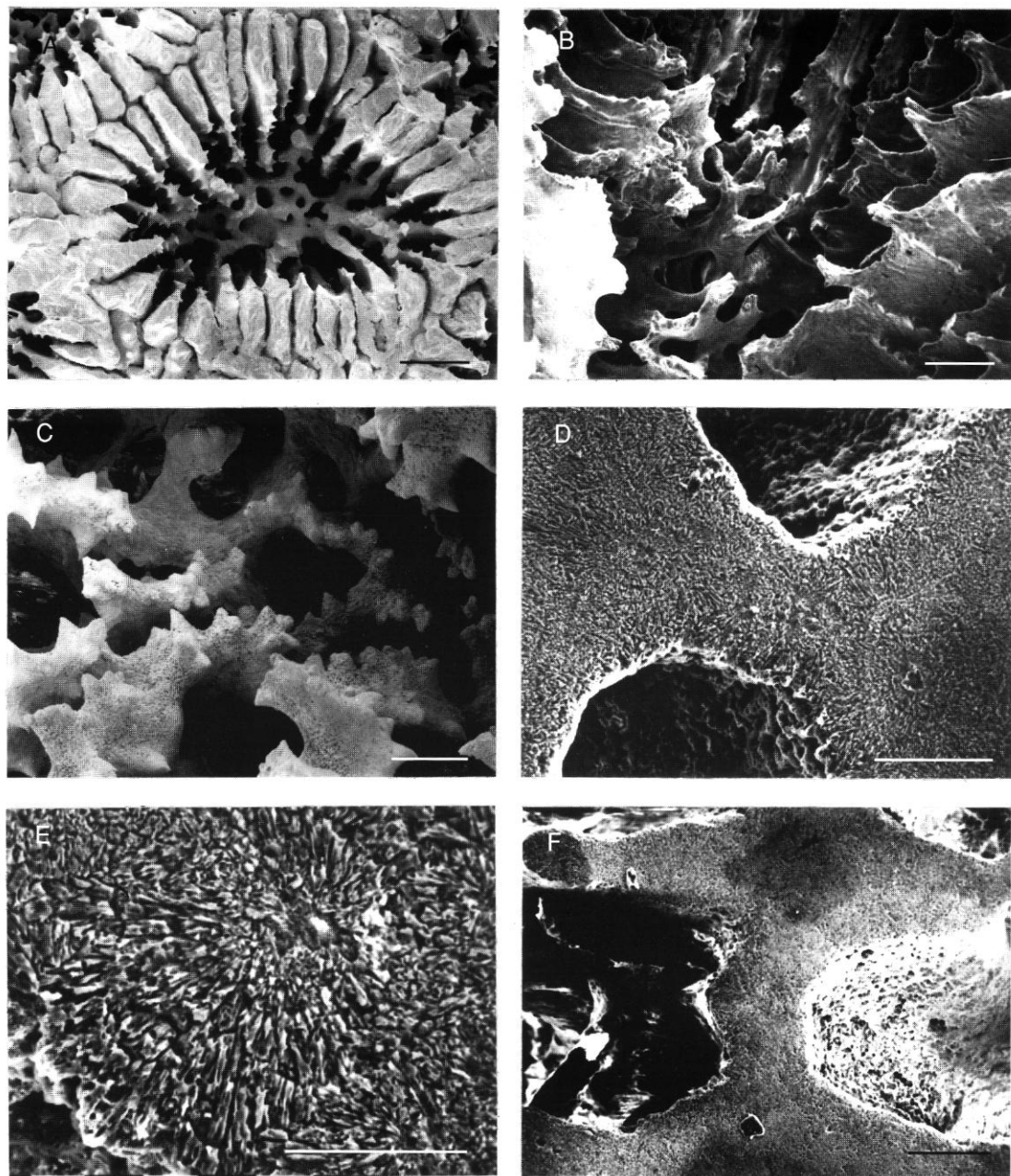


FIG. 9. — *Favia fragum* (Esper, 1795), SEM, columella and wall; **A**, specimen FAV560-4, view of a calice with spongy columella developed from fusion of axial septal margins; **B**, specimen 631, central part of calice with spongy columella resulting from twisting and tangling of axial teeth; **C-F**, specimen 1260: **C**, axial margins of septa and their relationship with columella; **D**, early stage of septothecal wall formation, lateral expansion of the neighbouring septa through adjunction of calcification centres; the large areas to left and right are septa; **E**, calcification centre and surrounding aragonitic fibres within the wall, detail of **F**; **F**, later stage of wall formation showing the development of a new radial element; structures at top and bottom are septa. Scale bars: A, B, 1 mm; C, 200 μ m; D-F, 100 μ m.



FIG. 10. — *Favia fragum* (Esper, 1795), successive stages of wall formation, traced from SEM photographs of specimen 616, axial part of calice is beyond the top of A, B and C; **A**, early stage of wall formation just after junction of both lateral expansions from neighbouring septa, note the calcification centres broadly arranged in line parallel to the wall and the small notch on the external margin of wall indicating the point of junction; **B**, thickening of wall by adjunction of calcification centres on its internal side, see also Fig. 9D; **C**, later stage of wall formation showing the earliest calcification centres aligned parallel to the wall and the later centres arranged perpendicular to the wall and contributing to the formation of a new septum, see also Fig. 9F. Scale bars: 100 μ m.

stood, they obviously correspond to starting points of aragonite fibres. Therefore, their distribution in space and time strongly controls morphological and structural development of coral skeleton. SEM observations of slightly etched transverse sections of septa and walls of *Favia fragum* show calcification centres as non-fibrous crystallized structures contrasting with the surrounding incremental layers of aragonite (Fig. 12A, B). It should be noted, however, that the appearance of these centres is highly variable according to sample preparation and is particularly sensitive to etching conditions (Fig. 12). Analysis of *Favia fragum* skeleton shows that septal and costal micromorphologies, as well as the

columella and septothecal wall are structures directly depending on the three-dimensional location of calcification centres. Centres described from thin sections in previous works (Alloiteau 1957; Zlatarski & Martinez Estalella 1982) appear as dark large dots (Fig. 13C) or as series of centres forming a dark line when septal teeth are inclined to the axial margin. SEM observations, however, show these previously described large dots correspond in fact to groups of centres approximately aligned normal to the septal plan. This arrangement occurs both in septa and costae but is also involved in formation of the columella and the septothecal wall. This therefore seems to reflect the skeletal growth process of *Favia fragum*.

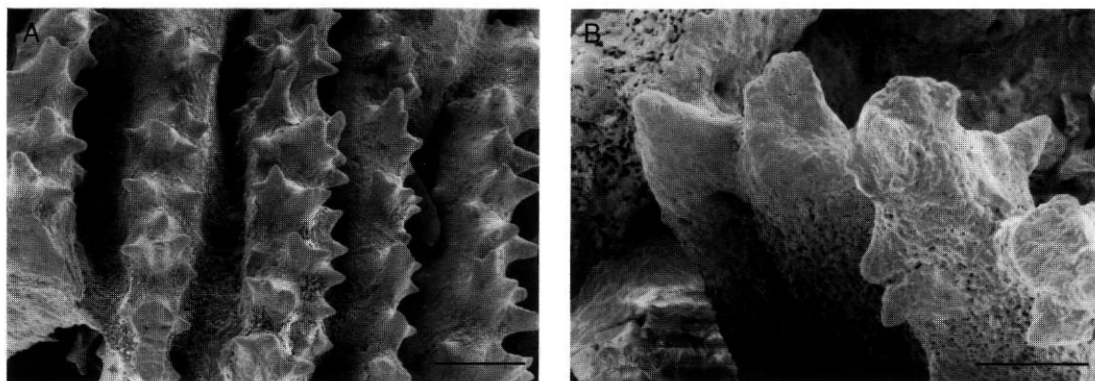


FIG. 11. — *Favia fragum* (Esper, 1795), SEM, costal dentation; **A**, specimen 616, well-developed costae with costal teeth bearing group of points; **B**, specimen FAV560-2, costal dentation showing simple conical teeth on the left. Scale bars: A, 200 μ m; B, 100 μ m.

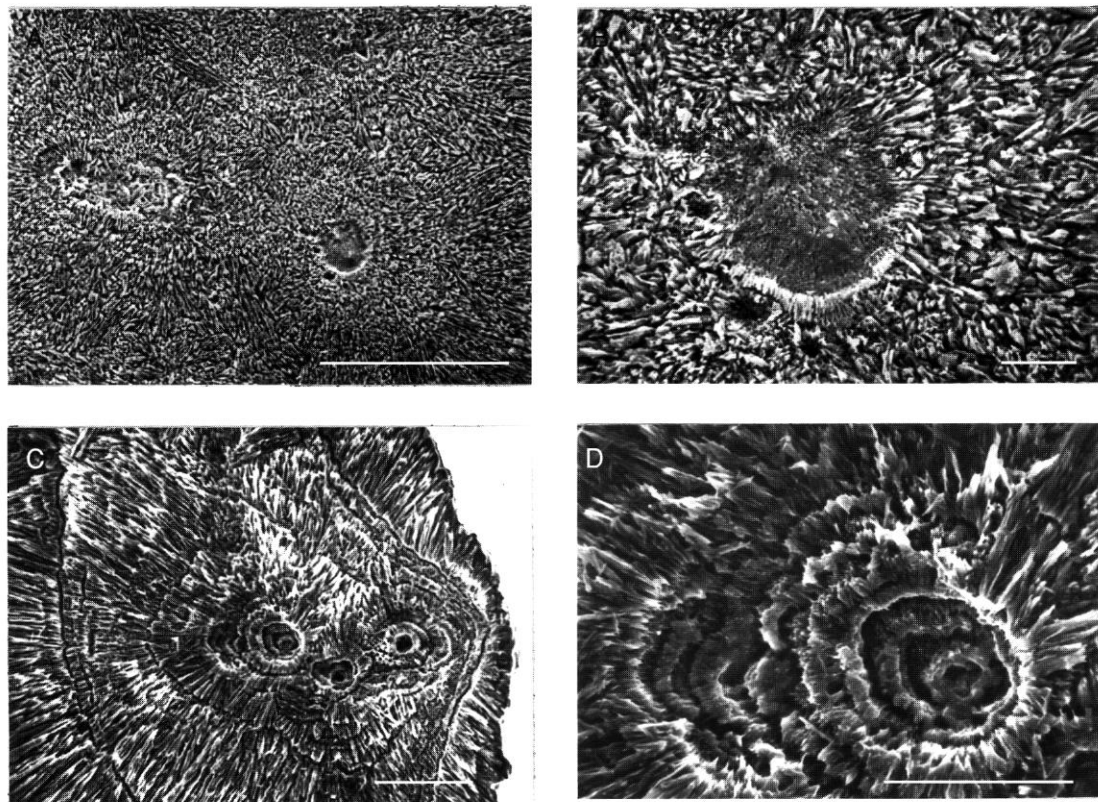


FIG. 12. — *Favia fragum* (Esper, 1795), SEM, calcification centres; **A**, specimen 616-2, transverse section slightly etched for 40 seconds with a solution of formic acid 1% and glutaraldehyde 3%; **B**, detail of A, same preparation, calcification centre clearly appears as non-fibrous crystalline structure; **C**, specimen 631, transverse section prepared with an enzymatic solution of alcalase pH 7.5 for 3 hours 35 minutes, calcification centres and their immediate surrounding incremental layers are strongly etched; **D**, detail of C, same preparation, internal structure of calcification centre cannot be seen from this type of preparation. Scale bars: A, C, 100 μ m; B, 10 μ m; D, 50 μ m.

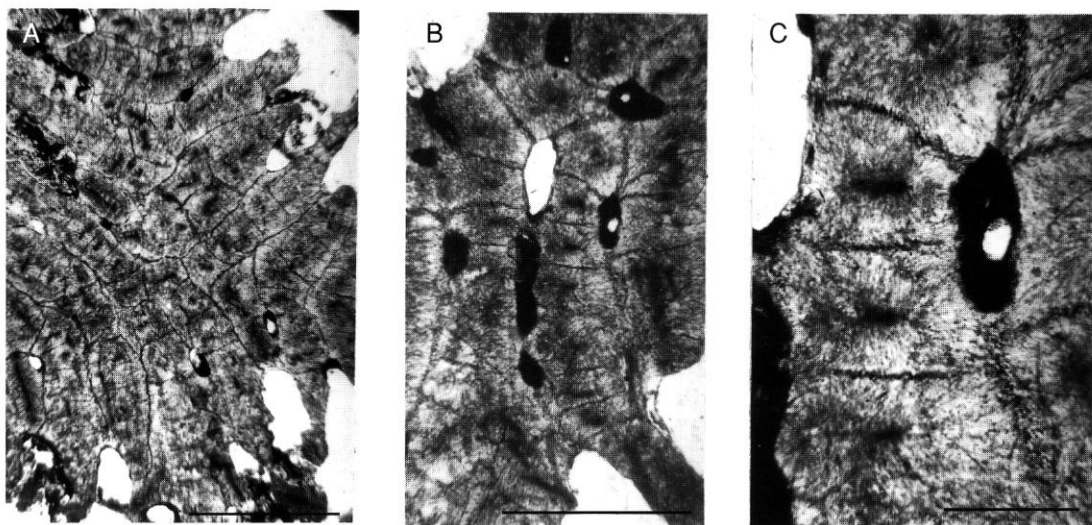


FIG. 13. — *Favia fragum* (Esper, 1795), thin sections from the Alloiteau Collection, MNHN Paléontologie; **A**, S12451a, transverse section in the wall area; **B**, S12451b, transverse section showing the wall and the peripheral part of calice; **C**, detail of B. Scale bars: A, 1 mm; B, 500 µm; C 200 µm.

SKELETAL GROWTH

Development of coral skeleton results from incremental growth shown by concentric layers of fibrous aragonite around calcification centres. This forms groups of points occurring at tooth ends of distal margin of septa and costae, each point resulting from growth around a calcification centre. Paddle structures are therefore formed from regularly aligned calcification centres, the arrangement of points at distal margin reflecting the arrangement of these centres within the septal microstructure. Series of centres are parallel to growth direction and branched axis of calcification centres was never observed.

Length of aragonitic fibres, and therefore thickness of incremental growth layers, vary according to growth direction. This differential development of aragonite crystals leads to the burial of previously formed points on the lateral septal faces and also to the gradual infilling of space between neighbouring teeth along the distal margin of septa (Fig. 8).

SEM observations of the distal septal margin show that aragonitic crystals within sets of fibres are clearly oblique to the external surface of sep-

tum (Fig. 6) contrary to the widely accepted view that fibres are perpendicular to the basal ectodermal layer.

DISCUSSION

To date, the Milne Edwards specimens of *Favia fragum* may be regarded as the oldest available material relevant to the historical development of its species definition. Moreover, the first descriptions of septal and thecal microstructures of *Favia fragum* (Alloiteau 1957; Zlatarski & Martinez Estalella 1982) both included morphological observations of the Milne Edwards specimens.

From the generic characterization by Milne Edwards (1857: vol. 2, 426) to the latest treatment by Veron (1986: 450), morphological relationships between adjacent corallites have been used to discriminate between *Favia* and related genera. For both authors, colonies belonging to *Favia* are plocoid while *Favites* Link, 1807, the closest genus, is characterized by cerioid colonies. Variability of this geometrical arrangement leads

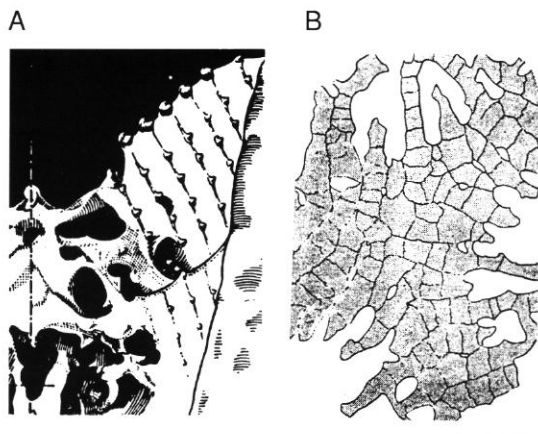


FIG. 14. — *Favia fragum* (Esper, 1795), original figures from Alloiteau 1957; **A**, septal ornamentation (Alloiteau 1957: fig. 98); **B**, transverse section of septothecal wall at the junction of four calices (Alloiteau 1957: fig. 96). Scale bar: A, no scale; B, 1 mm.

Veron (1986: 451) to consider, however, that the generic distinction based upon plocoid *versus* cerioid arrangement may be somewhat “arbitrary”. This is well illustrated by the variability in calicinal pattern in Milne Edwards’ specimens. The budding process giving rise to “equal corallites” in *Favia* and to “corallites of different size” in *Favites* is also regarded by Veron (1986) as a subsidiary distinctive character.

This established use of purely morphological characters for defining supra specific taxa has to be related to diverse comments on the unsatisfactory state of classification of *Favia* and related genera (e.g. Vaughan 1918) and to the paradoxical remark of Veron (1986: 445), considering the family Faviidae, that sometimes “species may be more readily recognized than genus”.

The first attempt to introduce additional criteria at generic level was made by Alloiteau (1957: 138), who accurately described the micromorphology of septal growing edges, the ornamentation of septal sides of *Favia fragum* (Alloiteau 1957: fig. 98) (Fig. 14A) and also made the first observations concerning septal microstructure. Curiously, little was done in this study for coordinating all morphological and microstructural data which are presented separately. Because of recent improvements in understanding the mechanisms of invertebrate

biomineralization and improved imaging which facilitates comparison of similar-scaled pictures of micromorphology and microstructure, it is now possible to integrate all morphological and microstructural data on *Favia fragum* within a single description of its skeletal growth.

The basic unit controlling septal organization within the colonies of the Milne Edwards Collection is the denticulate group of calcification centres whose typical arrangement is best seen on the middle part of distal septal margins. As internal arrangement of these basic growth units does not correspond to any previously-described type of trabeculae, we prefer to describe the microstructure for itself without referring to usual terminology. Each growth unit comprises up to six or seven centres arranged in a transverse alignment normal to the septal plan. The most lateral of these centres are not completely buried by the further growth of fibres during the later stages of septal development and therefore remain visible on the lateral faces of septa. This is the origin of the series of granules illustrated by Alloiteau (1957: fig. 98) (Fig. 14A) and regarded by him and later by Zlatarski & Martinez Estalella (1982) as lateral ornamentation. However, these series of granules, the strength and continuity of which depend on the regularity of the growth process, have to be considered as part of the basic septal plan and not as ornamental (= superficial) features. At this point, attention must be drawn to the possible misinterpretation that may result from observation of the septal faces alone. In particular, linear series of granules may be produced by a number of different septal microstructures (cf. description of septal structure in *Montivaltia* Lamouroux, 1821 (Gill & Lafuste 1971). Only relevant comparison between septal face morphology, septal growing margins (where first stages of calcification are seen) and septal microstructures allow septal organization to be correctly understood.

As already mentioned in the above descriptive part, the basic growth unit of septa in *Favia fragum* may be composed of a variable number of calcification centres, which gives rise to a first level of variability between septa of successive cycles within the same calice and between septa of different corallites. From this point of view,

specimen 631 appears remarkable for its regularity and the well-expressed organization of its septal margins. In other specimens, despite a high morphological variability in size and shape of calices, the same basic structure of septal growth units occur. The variability in number and development of calcification centres in each growth unit cannot be attributed to subspecies distinctions or to controlling ecological parameters since these are unknown for the Milne Edwards specimens.

The range of microstructural variability may be clearly assessed by taking into account changes of microstructural features at the distal ends of septal growth units from the axial septal margin to the costal margin. At the axial septal margin, the basal parts of septal growth units become very elongated, leading to the formation of digitiform septal extensions (Fig. 5A-C, called "axial teeth" by previous authors (Alloiteau 1957; Martinez Estalella 1982). As mentioned by these authors, the spongy columella is exclusively built by these septal expansions, and this agrees well with our own observations (Fig. 9A-C). However, these "axial teeth" should not be regarded as distinct features of septal architecture. Round calcification centres are clearly seen on their tips and continuous growth axes occur within their elongated parts. This indicates that their internal structure and therefore their growth pattern, are basically the same as for typical septal growth units of the middle part of septal margins. Clearly, "internal teeth" of other authors result from only slight modifications in growth pattern of the basic septal units.

Different patterns of growth variation can also be observed on the costal margins and are mainly due to variations in the degree of development of costal teeth and to a reduced number of points at their distal ends (Fig. 11). In all cases, however, the same basic scheme of the septal growth unit can be recognized.

In his introductory chapter to the family Faviidae, Veron (1986: 443) qualified the septal structure of these corals as "simple". In the *Treatise of Paleontology*, Wells (1956: F400) regarded the simple trabeculae as a diagnostic criteria for the subfamily Faviinae. Analysis of Milne Edwards specimens of *Favia fragum* sug-

gests that this cannot be applied to the septal structure of this "key species". First, accurate observation of septal arrangement shows that, in spite of the morphological differences and varied origins of the specimens, the basic septal architecture remains the same. Secondly, the arrangement of calcification centres within individual growth units always shows a polycentric pattern, excluding a simple trabecular structure. As the alternative term of compound trabeculae may include very different microstructural arrangements, these would have to be analysed before reassessing the significance of polycentric patterns. Finally, this three-dimensional arrangement resulting from precise positioning of calcification centres and permanent control of fibre growth direction, is strictly maintained during successive growth stages, whatever growth unit is considered.

CONCLUSION

By using and comparing both morphological and structural data on different scales within and between the studied colonies of *Favia fragum*, a preliminary assessment of potentially diagnostic criteria can be made.

Characters with a relatively high potential for skeletal plasticity are those related to the external geometry of calices including their size and shape, their relationships with surrounding calices, the length of costae and abundance of coenosteum. To a lesser degree, some intracalicular elements may also vary in size and detailed shape, i.e. columella and distal dentation of septa. Variation of wall aspect appears to be related to the successive stages of wall formation and therefore is directly dependent on septal development. Constant characters that may be used as discriminating criteria for taxonomy include number of cycles and budding process, but also distribution and arrangement of calcification centres which control three-dimensional growth process and therefore, micromorphology. These results emphasize the need for taxonomic studies combining the 2D-analysis of scleractinian micro- and ultrastructure with 3D-observations of micromorphology and morphology. This inte-

grated approach can be used to obtain a better understanding of the growth process and its control. It also appears more promising than basing scleractinian taxonomy only on analogies and on differences of shape and macromorphology.

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